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Agricultural Memorandum No.696

ON THE SYNTHESIS OF TEMPERATURE DEPENDENT BIOLOGICAL DATA

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1. Much biological reporting, if not anecdotal, remains essentially descriptive. Whilst there have been some notable attempts to arrive at deterministic models of response to impressed environmental elements, nevertheless, most numerical analyses settle for lower order associations (correlations). One reason for this possibly follows from the spread of genetic make-up, and from the survival value to a species, of a spread of response within a population, to imposed environments.

To the worker more used to dealing with purely physical systems, the apparent breakdown in biological systems of balance equations, of equalities and of 1 to 1 relationships can be disturbing; but once the inherent variability of biological samples is accepted, it need not hinder the search for unifying approaches nor detract from the value of an energy balance approach.

2. To the physical scientist, the association of a fairly precisely defined energy requirement or change in chemical constitution, with each particular phase of an organisms development or life cycle, would seem a quite natural expectation. This may oversimplify the biological situation, but the idea cannot be rejected out of hand.

A common and universal index of exposure to temperature is the Degree Day summation above some nominated base or threshold temperature. Such summations do not always lead to a constant requirement for a particular phase of growth. Agricultural Memorandum No.622 introduces Metabolic Change units as a alternative index of exposure, and at the same time, through its link with reaction rates, suggests some insight into the mode of action of the organism.

The purpose of this paper is two-fold

(i) to provide a spread of examples for poikilotherms that examine the applicability of the Metabolic Change unit approach,

(ii) to demonstrate how laboratory studies at constant temperature, for economically important species may be analysed and then synthesised, so that the transfer to variable temperature regimes and the field situation can be made.

If real-time modelling of the progress of pests and diseases is seen as one end point, then such work constitutes a necessary precursor.

3. Three basic modes of response to temperature are examined through their associated Q_{10} value and beyond that, through the nature of the implied, internal controlling process. These modes are set out schematically in Figures 1 and 2.

Figure 1 considers an exponential, a linear, and a parabolic response to temperature.

3.1. An exponential response is characteristic of a first order chemical reaction. Q_{10} is essentially greater than 1 and commonly of the order 2 - 3.

With $f = e^{k}$

where k = reaction rate

= linear function of temperature T

= C + MT (where C, M are constants)

then $Q_{10} = f_{b+10} / f_b$

$$Q_{10} = 1 + \frac{1}{f_b} \cdot \frac{\partial f}{\partial T} \cdot 10$$

$$Q_{10} = 1 + 10. \frac{\partial k}{\partial f}$$

Q_{10} = constant > 1. cf. Figure 2.

Obviously biological systems will place restrictions over and above those that would hold for purely chemical systems, for example, through the action of threshold temperatures necessary for particular processes to become initiated or dominant, and through limitations on the range of temperatures that prove acceptable.

3.2 A linear response to temperature is a not an uncommon observation. Q_{10} decreases with temperature. By implication, more than one process might be expected to be operative at the same time. The dominant process would be expected to be primarily chemical at low temperatures (Q_{10} large) and primarily physical at high temperatures, ($Q_{10} \rightarrow 1$), for example a diffusion or mass flow process.

With $f = c + m\,T$

$$Q_{10} = f_{b+10} / f_b$$

$$Q_{10} = 1 + \frac{1}{f_b} \cdot \frac{\partial f}{\partial T} \cdot 10$$

$$Q_{10} = 1 + \frac{10.\ m}{c + mT}$$

and as T increases, $Q_{10} \rightarrow 1$; cf. Figure 2.

3.3. A parabolic response to temperature is exhibited by all organisms, in the limit. This is the reflection of a range of temperatures within which the organism is well accommodated and maximum productivity is achieved; outside of this range, physiological and behavioural processes of survival value are called into play, and if extremes of temperature persist for any length of time, they are likely to prove lethal.

With $f = mT - nT^2$

$$Q_{10} = f_{b+10} / f_b$$

$$Q_{10} = 1 + \frac{1}{f_b} \cdot \frac{\partial f}{\partial T} \cdot 10$$

$$Q_{10} = 1 + 10\left(\frac{m-2nT}{mT-nT}\right)$$

$$Q_{10} = 1 + \frac{10}{T} - \frac{10n}{m-nT}$$

At the vertex $T = m/2n$ and $Q_{10} = 1$

with $T > m/2n$ $Q_{10} < 1$ cf Figure 2

4. A selection of examples of temperature and metabolic change unit summations now follows. The choice is made at random from literature made available for other purposes.

4.1 Rate of development in embryos of a cypridont fish exposed to different temperature - salinity - oxygen combinations

Kinne, O 1962 Canadian Journal of Zoology

Kinne, E M Vol. 40, pp.231 - 254

The basic data used are reproduced in Table X (the original table numbering)

TABLE X

Incubation period in days (i) and percentage mortality (m) at different constant temperatures in fresh water

T°C	i (days)	m(%)
15.0	32.0	20
18.0	17.0	33
19.0	14.5	33
19.0	14.0	25
19.0	14.0	41
20.0	12.5	26
20.0	13.0	50
24.0	9.5	50
24.0	9.0	60
24.0	8.5	71
25.0	8.0	40
25.0	7.5	91
25.0	8.0	77
27.5	6.0	79
27.5	6.0	83
28.0	-	100
28.0	-	100
29.0	-	100

An upper limit to incubation is obviously set at 28.0°C. Other information in the article suggests a lower limit of 12.0°C.

Day Degree summations are made for the incubation periods of Table X above a base of 12°C. Metabolic Change units are calculated for the same data using a Q_{10} value of 3.0 and the same base temperature. This information is shown in Table X.1.

TABLE X.1.

Day Degree and Metabolic Change unit summations for the data of Table X

T°C	i (days)	Day Degrees	Metabolic Change Units /K_b
15.0	32.0	96	51 (42)
18.0	17.0	102	37
19.0	14.5	101	35
19.0	14.0	98	34
19.0	14.0	98	34
20.0	12.5	100	33
20.0	13.0	104	34
24.0	9.5	114	40
24.0	9.0	108	38
24.0	8.5	102	36
25.0	8.0	104	38
25.0	7.5	97	36
25.0	8.0	104	38
27.5	6.0	93	38
27.5	6.0	93	38
	Mean	101	37
	Standard Deviation	5.4	3.0

The first calculation of Metabolic Change units above the threshold temperature adopted (12°C) is obviously out of line with the remainder of the data. If for temperatures close to the threshold, a lower Q_{10} value of 2.0 is adopted, then a value (42) is obtained which is consistent with the remaining information and a constant value of the Metabolic Change units required for incubation to be completed.

The Day Degree summations also indicate a constant requirement before incubation, though the population shows a greater dispersion than for Metabolic Change summations. To this extent, the Metabolic Change approach gives some insight into the process implicit in the Day Degree approach in this instance, and to the situations where it is likely to be valid and useful.

4.2 Diapause potential in tropical flesh flies

Denlinger, D L 1974 Nature Vol. 252 pp 223-4

Duration of diapause in P.spilogaster is stated as lasting.

234.6 ± 6.8 days	at 12°C	constant temperature
100.9 ± 2.2 days	at 15°C	
72.6 ± 2.9 days	at 18°C	

Extrapolation would suggest a base temperature of around 10°C below which diapause would extend over more than a year, and an environment for which this species was not adapted.

We calculate Day Degree summations and Metabolic Change units above a base of 10°C for this information. Following the clue given by the analysis of data of section 4.1, it would seem reasonable to adopt a lower Q_{10} value at temperatures close to the threshold value (10°C), than for higher temperatures. A Q_{10} value of 1.5 is allocated at 12°C and a Q_{10} value of 4 at higher temperatures.

TABLE

Day Degree and Metabolic Change unit summations for the duration of diapause of P.spilogaster.

T°C	D.D	Metabolic Change units $/K_b$
12°	469	257
15°	505	250
18°	581	246
Mean	518	251
Standard Deviation	60	6

The flexibility of the Metabolic Change summation enables a constant quantity to be allocated to the duration of diapause.

Diapause initiation

An energy balance approach enables diapause initiation and termination for the tropical (as distinct from the temperate zone) species to be discussed in a quantitative way.

In the reference, a threshold (base) temperature of 20°C is demonstrated for pupal diapause initiation. It is indicated that diapause initiation is influenced by earlier exposure to temperatures above the threshold of 20°C, and that exposure to high temperature (eg 25°C) prior to exposure to low temperatures (eg 15°C), modifies the percentage of flies entering diapause. If the processes above and below the threshold temperature of 20°C are seen as acting in the opposite sense, for example by increasing or decreasing enzyme amounts, then it should be possible to indicate the exposure to high temperatures necessary to avoid diapause.

For induction of diapause, the requirement is given as 1-2 weeks at 15°-18°C mean daily temperature.

The requirements for diapause initiation in terms of Day Degree summations below 20°C and Metabolic Change unit summations below 20°C are seen as

1 week at 15°C	≡	35 Day Degrees	or 17.5 Metabolic Change units/K_b
2 week at 18°C	≡	42 Day Degrees	or 22.4 Metabolic Change units/K_b
Mean	~	40 Day Degrees	~ 20 Metabolic Change units/K_b

The incidence of pupal diapause of larvae held at 25°C for different periods after larviposition, and then transferred to 15°C is shown in the following table, together with the Day Degree summations and Metabolic Change accumulations over the period of exposure to high temperatures.

TABLE

Days at 25°C	Day Degrees	Metabolic Change unit/K_b	% entering diapause
0	0	0	85%
1	5	2.5	80
2	10	5.0	70
3	15	7.5	40
4	20	10.0	25
5	25	12.5	10
6	30	15.0	5
7	35	17.5	2
8	40	20.0	0

In both approaches the change accumulated in 8 days at the higher temperature is just sufficient to counterbalance the change induced by the exposure to cold that is necessary for diapause initiation.

Diapause termination

The tropical variety of P. spilogaster (in contrast to the temperate zone variety) have the ability to terminate diapause if exposed to high temperatures for a short period.

The percentage of larvae terminating diapause after spending 10 days at 15°C and then being transferred to 25°C for different periods is shown in the following table, together with the Day Degree and Metabolic Change units accumulated at the higher temperature.

TABLE

Days at 25°C	Day Degrees	Metabolic Change Units/K_b	% breaking diapause
1	5	10	20%
2	10	20	20
3	15	30	80
4	20	40	95
5	25	50	95
6	30	60	95

The changes accumulated in the initial 10 days exposure to cold are those appropriate to 50 Degree Days and 25 Metabolic Change units /K_b respectively. In an energy balance approach, these quantities would be expected to be counterbalanced by 10 days and 2.5 days exposure to high temperatures of 25°C respectively. The table above shows that the Metabolic Change unit approach is the more valid.

4.3 The effect of weather and emergence and take-off of overwintering Limothrips cerealium Haliday Thysanoptera.

T Lewis 1963 Ann. appl. Biol. Vol 51, pp. 489-502

Emergence

The emergence of thrips from bark brought from the field in the late spring to constant temperature laboratory conditions are shown in the following Table 1.

TABLE 1

Temperature °C	Duration of emergence	Days before 50% emergence
25°C	10 days	3
20°	14	5
15°	28	14

The spread of response implied by such data is very large. The corresponding Day Degree and Metabolic Change unit summations above an arbitrary base of 5°C are shown below in Table 2. A Q_{10} value of 4 has been adopted.

TABLE 2

Temperature	Day Degrees Complete emergence	Day Degrees 50% emergence	Metabolic Change units/K_b Complete emergence	Metabolic Change units/K_b 50% emergence
25°C	200	60	160	48
20°	210	75	112	40
15°	280	140	112	52
Mean	230	92	128	47
Standard Deviation	39	34	22	5

Flight maturation period

During hibernation many thrips appear to lose their ability to fly and regain it only after passing through a flight-maturation period that is temperature dependent.

From graphs in the paper we may develop the table below

TABLE - Flight maturation period
Number of days at constant temperature for 50% thrips to take off

Temperature	Days	Degree Days	Metabolic Change units/K_b
25°C	3	60	48
20°	5	75	40
15°	11	110	44
10°	30	150	60 (42)
Mean		99	43
Standard Deviation		35	3

An arbitrary base temperature of 5°C has been used, together with a Q_{10} value of 4. This at 10°C leads to a Metabolic Change unit value of 60. If as in previous examples, a lower Q_{10} value is adopted for temperatures close to the lower limit

for development, then it is possible to derive a constant requirement for this particular phase of the insect. A Q_{10} value of 2 at 10°C leads to a Metabolic Change unit value of 42.

4.4. Beitrage zur Kenntris der Blattlaus Myzus (Myzodes) persicae Sulz., Ubertragerin der Blattvollkrankheit der Kartoffel.

P Fenjves 1945 Bull. Soc. Entomologique Suisse
Bd. XiX, Heft.11, pp 489-611

Initial interest centres on Table 4.

TABLE 4

Effect of Temperature on larval development period (summer forms only)

Temperature °C	No. of insects	Development period (days) Mean	Min.	Max.
2.9°C	10	0	-	-
6.2	1	43.0	-	-
9.9	20	24.5	20	31
13.5	22	17.0	14	19
15.2	26	15.0	13	16
18.0	46	10.0	9	11.5
21.2	27	7.5	7	10.5
25.0	17	8.0	6	11
28.3	5	11.0	9	13.5
30.0	0	-	-	-

A threshold temperature for development is indicated in the reference as 4.3°C. An upper limit is set between 28°C and 30°C.

If Day Degree and Metabolic Change unit summations above this base temperature are made for the data of Table 4 we derive the information set down in Table 4A.

TABLE 4A

Day Degree and Metabolic Change unit summations for larval development period.

Temperature	Development Period Days	Day Degrees	Metabolic Change units/K_b
6.2°C	43	82	59
9.9	24.5	137	52
13.5	17	156	48
15.2	15	163	53
18.0	10	137	52
21.2	7.5	127	54
25.0	8	166	82 (57)
28.3	11	264	178 (59)
30.0	-	-	
Mean		154	54
Standard Deviation		55	3.6

The increase in development period that takes place between 21°C and 25°C (after 23°C say) becomes more marked beyond 25°C and as an upper, lethal temperature is approached. Obviously the response to temperature can be represented by the parabolic form set out schematically in Figure 1.

The conventional derivation of Metabolic Change units (above a base of 4.3°C) leads to the inconsistent values of 82 and 178 units at 25.0°C and 28.3°C respectively, that are shown in Table 4A, where a Q_{10} value of 3 has been adopted.

Three distinct Q_{10} values would appear in general to be called for, the first valid for the greater part of the temperature range to which a species is accommodated, the second valid close to the lower temperature limit and the third valid as the upper temperature limit is approached.

If above 23°C, a Q_{10} value of $\frac{1}{3}$ is adopted, from a base of 23°C (at which $K = 8.2\ K_b$, where K_b = reaction rate at 4.3°C), then the bracketed figures of Table 4A are obtained, and a uniform Metabolic Change requirement for the larval development period.

The item next of interest is contained in Table 9.

TABLE 9

Effect of temperature on the number of young larvae produced and on the life span

Temperature °C	Number of insects	Life span (Days)	Productive Period (Days)	Total young larvae
9.9	1	69	18	19
15.2	7	61	28	52
18.0	26	52	26	64
25.2	4	21	11	37
28.0	1	16	4	12

We may compute the Degree Day and Metabolic Change summations over the productive period using the Q_{10} values adopted in Table 4A, and also the accumulation associated with the production of a single larva. This information is shown in Table 9A.

TABLE 9A

Day Degree and Metabolic Change unit summations over the productive period of Myzus persicae.

Temperature	Productive Period (Days)	Degree Days	Degree Days per larva	Metabolic Change unit/K_b	Metabolic Change unit/K_b per larva
9.9	18	101	5.3	38	2.0
15.2	28	305	5.9	99	1.9
18.0	26	356	5.6	136	2.1
25.2	11	230	6.2	71	1.9
28.0	4	95	7.9	22	1.8
Mean			6.2		1.9
Standard Deviation			.9		.1

Some information in Tables 4 and 9 may be brought together as in Table 4/9 below:

TABLE 4/9

Temperature °C	Total Life Span (Days)	Larval Period (Days)	Productive Period (Days)	Balance of Life Span (Days)
9.9	69	24.5	18	26.5
15.2	61	15.0	28	19.0
18.0	52	10.0	26	16.0
25.2	21	8.0	11	2.0
28.0	16	11.0	4	1.0

If a lower Q_{10} value of 2 is adopted for the non-developmental, non-productive phase of the aphid's life, than that employed in Tables 4A and 9A (where $Q_{10} = 3$) then the associated Metabolic Change unit summations are shown in Table 4/9A.

TABLE 4/9A

Temperature °C	Balance of Life Span (Days)	Metabolic Change units/K_b
9.9	26.5	41.3
15.2	19.0	41.4
18.0	16.0	43.8
25.2	2.0	14
28.0	1.0	6

If the results at temperatures in excess of 23°C are dismissed as either being inappropriate, or because mean daily temperatures in excess of 23°C are not a usual phenomenum in the UK, then for practical purposes we may presumably associate a constant Metabolic Change accumulation with the non-developmental, non-productive phase of the aphid's life.

The Metabolic Change unit summations for the various phases of this economically important insect then suggest

Larval development phase – a constant requirement.
Reproductive phase – a constant requirement for each larva produced, but a variable requirement in total.
Balance of life span – a constant requirement.

Since the relationship between duration of reproductive phase and temperature shown in Table 9 may obviously be fitted to a parabolic curve, the possibility exists of estimating the time duration of the reproductive phase from temperature data, at least closely enough to produce working solutions. If for example mean daily temperatures are themselves summed and meaned progressively from a nominated starting date, the aphids entering their productive phase on the first day might be expected to terminate it when the number of days in the temperature summation just exceeds the duration to be inferred from the mean temperature of the period of calculation.

If Metabolic Change units calculated for daily (or shorter) periods may be summed to contribute to, and determine, the various phases of the aphid life cycle, then we have a basis for following the changes in aphid numbers from real-time weather data alone, other factors being equal.

5. The Metabolic Change unit summation approach has been shown to be of wide ranging application and to help in the analysis of situations where the conventional Day Degree summation provides no guide lines.

The Metabolic Change approach provides some insight into the mode of response of the organisms to temperature and to the nature of the internal processes involved.

The demonstrable association of a constant number of Metabolic Change units with particular phases of the life cycle of some organisms opens the possibility of moving, from the constant temperature laboratory situation to the variable temperature field situation, and beyond that to the monitoring (and prediction) of biological populations from a synthesis of conventional weather data.

The fact that some progress has been made in extending an energy balance approach to poikilotherms (as distinct from homeotherms, where the principle has general acceptance), must be a cause for some satisfaction.

Meteorological Office
Cambridge

January 1975

FIGURE 1

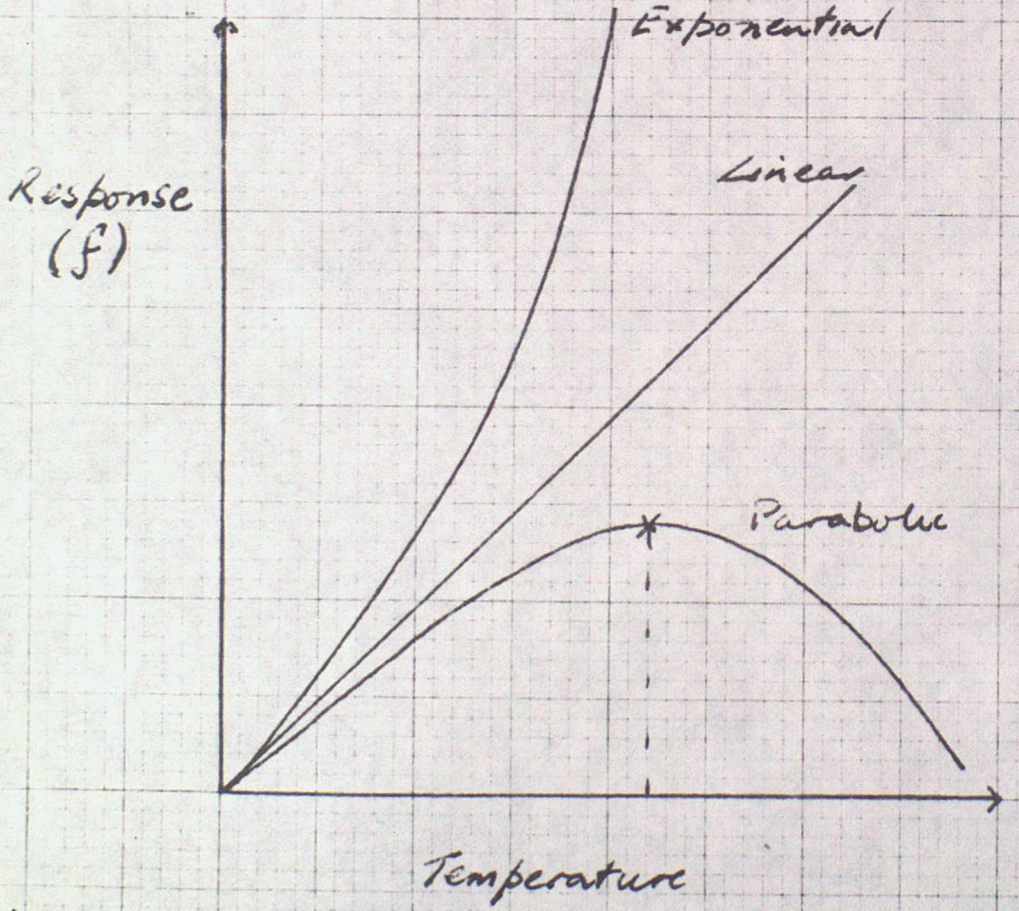

FIGURE 2